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THE EFFECT OF EXTENT OF DISTRIBUTION ON SPECIATION

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WHILE engaged in some research work on the geographic distribution of mammals under the supervision of Professor H. D. Reed at Cornell University in the fall of 1910 and the spring of 1911, certain conceptions regarding the relation between extent of distribution and the generic and specific modifications of mammals were brought to light. Due to the valuable and helpful criticism of Professors C. A. Kofoed and J. C. Merriam, and Dr. J. Grinnell, and of other members of the University of California, and to the advice and aid of Professor C. A. Kofoed, the rather vague ideas then formed have been worked over and crystallized into their form as presented in this paper.

In the past, much of the work that has been done on zoogeography has dealt with a study of the facts of distribution, both present and past, as they stand, together with a study of the factors influencing distribution and speculations regarding the explanation of some of the interesting and apparently anomalous facts thus brought to light. In all of this work, the distribution of animals has been considered almost entirely as the effect of certain biological and geological causes. The present paper is intended to show that the distribution of animals is not only the effect of other causes, but is in itself the cause of other effects, and that extent of distribution has a direct influence on the modification and speciation of the group concerned.

To find out how far-reaching and how potent is this effect, much further study is necessary, not only of the distribution of various groups, but of their classification and systematic relationships as well.

In brief, the effect of extent of distribution on groups of different systematic rank may be stated as follows: As the range of a group of animals, be it genus, family, or order, is extended, the species increase out of proportion to the genera, the genera out of proportion to the families, and the families out of proportion to the orders. In other words, if we assume that in a distributional area of certain extent, there are three genera and six species, in a distributional area of twice that size, there will not be six genera and twelve species, but more probably only four or five genera, and twelve species; *i. e.*, if in the first case the index of modification (a term here used to indicate the average number of species per genus) be two, in the second case it will be greater than two.

As new distributional areas are added, other factors remaining equal, there is a constant increase in number of species and subspecies, going hand in hand with a diminishing rate of increase in genera, the result being a constantly larger index of modification as the area inhabited by a group of animals is extended.

It should be remarked that a unit of area in this connection should be considered a distributional unit, not a geographical unit. In other words, while the addition of one hundred square miles might or might not involve a change in the life of a region, the addition of a new "life zone," "fauna," or association" (see p. 155) would inevitably involve a biotic change, and therefore the addition of one or several of any of these distributional areas should be considered as an addition of a unit, comparable to another unit of similar kind.

Two possible ways of testing this hypothesis present themselves. We may compare the faunas of distributional areas of dissimilar size, or we may compare the specific and generic differentiation found within families occupying areas of different extent. The former method we should expect to work out with a fair degree of accuracy, but the latter involves so many modifying circumstances that even if sufficient data were at hand, it would be difficult to prove anything by it. In the first place there is the difficulty of comparing, in a distributional sense, the areas occupied by different families, since, as pointed out above, the geographic areas do not necessarily coincide at all with distributional areas; in the second place, while it is justifiable to compare the speciation of a family in one region with the speciation of the same family in another region, it is of doubtful value to compare the speciation of one family with that of another in the same or different regions, unless the other factors controlling their speciation be comparable or nearly so. In view of this there are few families which could be advantageously compared with each other as to speciation in relation to extent of distribution, yet in the families which do seem to lend themselves to such a comparison, the evidence all points towards the correctness of the law here proposed.

The bats seem as favorable for such an interfamily comparison as any group of mammals that could be selected, and the table (Table I) of their distribution by

TABLE I
DISTRIBUTION AND SPECIATION OF FAMILIES OF CHIROPTERA
Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Vespertilionidæ.....	Cosmopolitan.....	17	190	11.18
Emballonuridæ.....	Warm parts of both hemispheres.....	15	79	5.27
Pteropodidæ.....	Old World.....	18	110	6.11
Rhinolophidæ.....	Old World.....	6	61	10.16
Nycteridæ.....	Warm parts of Old World.....	2	15	7.50
Phyllostomidæ.....	Neotropical.....	36	81	2.25

families is significant. One family, the Vespertilionidæ, is cosmopolitan, inhabiting every zoologic region and *every* life zone, and it has 11.18 species per genus, the highest of any family of bats. The Phyllostomidæ, on the other hand, has the narrowest range, occupying only the warm zones of one zoologic region, namely, the neotropic, and has in 36 genera only 81 species, giving 2.25 as the

TABLE II
DISTRIBUTION AND SPECIATION OF FAMILIES OF INSECTIVORA
Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Soricidæ.....	Palaearctic, Ethiopian, Oriental and Nearctic regions, all zones.....	11	125	11.36
Erinaceidæ.....	Palaearctic, Ethiopian, and Oriental regions.....	2	16	8.00
Talpidae.....	Palaearctic and Nearctic regions, temperate zones only.....	11	25	2.27
Tupaiidæ.....	Oriental region, warm zones.....	2	15	7.50
Macroscelidæ.....	Ethiopian region, warm zones.....	3	17	5.66
Potamogalidæ.....	Central Africa and Madagascar, tropical zones.....	2	3	1.50
Galeopithecidæ.....	Malay only, forests, tropical zones...	1	2	2.00
Chrysochloridæ.....	South Africa.....	1	7	7.00
Centetidæ.....	Madagascar.....	7	21	3.00
Solenodontidæ.....	Cuba and Hayti.....	1	2	2.00

index of modification. The other figures in this table are significant, but the indices of modification in the families Rhinolophidæ and Nycteridæ are abnormally large, and will probably be reduced by subsequent subdivision of genera, or discovery of new forms.

Table II shows the generic and specific differentiation

of the various families of Insectivores, but as some of the families have not been as intensively studied as others, and as the conditions affecting their distribution and speciation are so different in different families, we could hardly expect accurate results, and yet the table clearly shows a tendency for the families having wider ranges to have a higher index of modification, the almost cosmopolitan shrews, for instance, having 11.36 species per genus, and the families with restricted range (*Galeopithecidae*, *Solenodontidae*, *Centetidae* and *Potamogalidae*), having only 1 to 3 species per genus. The *Talpidae* and *Chrysochloridae* do not seem to conform in their speciation to what should be expected.

When the specific and generic subdivisions of all the families of mammals have been worked out more perfectly, and their ranges in a distributional sense, *i. e.*, through life zones, faunas, and associations, are more accurately known, some interesting facts concerning the relation between their indices of modification, and the extent of their ranges, might be brought out.

It is interesting to note that there is a considerable number of conspicuous examples of wide-ranging genera which are remarkably poor in species. Among carnivorous mammals there are many such cases, these animals seeming to be adaptable to an almost unlimited range of environmental conditions without modification, or, in other words, their germ plasm is not stimulated to change by altered conditions of climate or environment. The tiger, for instance, is equally at home in the bleak frozen steppes of Siberia, or in the hot humid jungles of India. The genus *Cynaelurus* is widely distributed over the Ethiopian and Oriental regions, and yet it contains but a single species, with several geographic races. Among birds there are a number of similar examples, the most striking case, perhaps, being *Pandion*, a cosmopolitan genus with but a single species. The same peculiar condition occurs among lower animals, as for instance in the Dinoflagellate genus *Diplopsalis*, which is cosmopolitan

TABLE IIIA

SPECIATION OF MAMMALS IN VARIOUS DISTRIBUTIONAL AREAS IN CALIFORNIA

Data from Grinnell (1913A), (1908), Grinnell and Swarth (1913)

Group	Boreal and Upper Transition Zones					
	San Jac. Mts. (350 Sq. M.)		San Bern. Mts. (550 Sq. M.)		Sierra Range (30,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata.....	1	1	1	1	2	4
Bovidae.....					1	1
Cervidae.....	1	1	1	1	1	3
Antilocapridae.....						
Rodentia.....	7	8	10	12	21	57
Sciuridae.....	4	4	5	5	6	22
Castoridae.....						
Aplodontidae.....					1	1
Muridae.....	2	3	3	5	7	17
Geomyidae.....	1	1	1	1	1	5
Heteromyidae.....			1	1	1	2
Zapodidae.....					1	2
Erethizontidae.....					1	1
Ochotonidae.....					1	3
Leporidae.....					2	4
Carnivora.....	6	6	2 (7)	2 (8)	14	21
Felidae.....	2	2	(2)	(2)	2	3
Canidae.....	1	1	1 (2)	1 (2)	3	6
Mustelidae.....	3	3	1	1	7	10
Procyonidae.....			(1)	(1)	1	1
Ursidae.....			(1)	(2)	1	1
Insectivora.....	2	2	2	2	4	11
Soricidae.....	1	1	1	1	2	7
Talpidae.....	1	1	1	1	2	4
Cheiroptera.....	2	3	2	3	4	7
Phyllostomidae.....						
Vespertilionidae.....	2	3	2	3	4	7
Molossidae.....						
Total.....	18	20	17 (22)	20 (26)	45	100
Indices of modification.....	1.11		1.17 (1.81)		2.22	

in warm and temperate seas, and yet is composed of not more than two species. No adequate explanation of these exceptional cases has been offered, and it is probable that their speciation, or lack of it, is due to conditions of their existence or constitution which we do not understand, or do not recognize.

To test the law by comparison of faunas of areas of different extent, a series of tabular comparisons of the faunas of various regions of different size and character was made. In all of these tabulations, care has been taken in the choice of areas for comparison to make them of unequal size from a distributional point of view, and to make them reasonably comparable. An arctic and a tropical region, for example, are not considered reasonably comparable as regards number of genera and species, nor is a region on the outskirts of the range of a group considered comparable with a region near its center of distribution.

Table III shows a comparison of the mammals of various parts of California. The regions compared are as follows: (*A*) the boreal and transition zones of (*a*) the San Jacinto Mountain range, (*b*) the San Bernardino Mountain range, and (*c*) the entire Sierra range, including the Warner and Shasta Mountains to the north, and the San Bernardinos and San Jacintos to the south; (*B*) a comparison of all the zones of (*a*) the San Jacinto Mountains with the immediately adjoining country, (*b*) the Sierra range as defined above, and including their foothills, and (*c*) the entire state.

A careful study of Table III brings out a number of interesting and significant facts, and bears out the law here proposed with unexpected accuracy, barring one seeming exception which, as we shall see later, can not truly be considered as such.

Let us compare first the three areas in which only the two uppermost life zones are involved, and from which the species invading only the lower Transition zone have also been excluded. First, a word as to the areas compared. The Boreal and Transition zones of the Sierras take in over one half of all the representation of these zones within the whole state. These zones of the San Bernardino and San Jacinto mountain masses are, as compared with the entire range, very small indeed, and comprise almost as small areas as could justifiably be

TABLE IIIB

(Data as above)

(Data as in Table IIIA)

Group	All Zones					
	San Jac. Mts. (2,500 Sq. M.)		Sierra Range (60,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata.....	2	2	3	7	4	10
Bovidae.....	1	1	1	2	1	2
Cervidae.....	1	1	2	5	2	7
Antilocapridae.....					1	1
Rodentia.....	16	41	28	110	31	203
Sciuridae.....	5	7	7	26	7	41
Castoridae.....					1	2
Aplodontidae.....			1	1	1	2
Muridae.....	5	14	10	33	11	64
Geomysidae.....	1	4	1	9	1	19
Heteromyidae.....	3	12	4	24	4	48
Zapodidae.....			1	2	1	5
Erethizontidae.....			1	1	1	1
Ochotonidae.....			1	3	1	3
Leporidae.....	2	4	2	11	3	18
Carnivora.....	9	10	15	29	17	51
Felidae.....	2	2	2	3	2	6
Canidae.....	3	4	3	9	3	17
Mustelidae.....	3	3	7	13	9	22
Procyonidae.....	1	1	2	3	2	4
Ursidae.....			1	1	1	2
Insectivora.....	3	3	5	12	6	20
Soricidae.....	2	2	3	8	4	14
Talpidae.....	1	1	2	4	2	6
Cheiroptera.....	4	7	7	12	11	26
Phyllostomidae.....					1	1
Vespertilionidae.....	4	7	6	11	8	21
Molossidae.....			1	1	2	4
Total.....	34	63	58	170	68	310
Indices of modification.....	1.85		2.93		4.56	

considered to be individual faunal units. The San Jacintos are somewhat smaller than the San Bernardinos, but the difference is almost inconsiderable when compared with the Sierras. Before examining the table, let us see

what conditions in number of genera and species would be expected in these three areas. The San Bernardinos, being almost as small a faunal unit as should be separately considered, we should expect to approach a minimum index of modification, *i. e.*, a minimum number of species per genus, approaching one as a limit. On the San Jacintos, these being smaller than the San Bernardinos, we should expect fewer types according to the law suggested by Grinnell and Swarth (1913), that the number of persistent types in a disconnected area varies directly with the size of the area. On the entire Sierra range we should expect, due to the greatly increased territory, a considerable increase in genera, but a very much greater increase in species. Looking now at Table III, we find that with the single exception of the carnivores on the San Bernardino Mountains, not one discrepancy exists. The Ungulates, Insectivores and bats are represented by the same numbers of genera and species on both of the small areas, and all of them show a marked increase in genera and species on the larger area, in every case with an increase in the index of modification.

The rodents, which show a larger degree of differentiation than any of the other groups, show a very interesting advance in the index of modification as the area is extended. The carnivores, as stated above, show a seeming discrepancy, inasmuch as there are six genera and six species existing on the San Jacintos, and only two genera and two species on the San Bernardinos, whereas, if they conformed with our laws of distribution, we should expect at least six, and possibly seven or eight, species to be found there. On page 35 of Grinnell's "*Biota of the San Bernardino Mountains*" (1908) we find reference to a number of carnivores now rare or extinct on the San Bernardinos, which undoubtedly have been exterminated by man within the last fifty years. Counting these forms, which it seems to me we are justified in doing, the table bears out the law without a single exception, not only for

the total of mammalian forms, but the totals for each order and for each family.

In comparing the three areas in which all the life zones are involved, the truth of the effect of extended distribution on speciation is still more forcibly impressed upon us. In this case we are comparing areas which are successively larger in size, the San Jacintos, with their foothills and low passes involving the fauna of an area of about 2,500 square miles, the Sierras, about 60,000 square miles, and the whole state of California about 158,000 square miles. The following table, derived from Table III, is very significant in showing the diminishing in-

Group	Genera			Species			Index of Modification		
	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.
Ungulates.....	2	3	4	2	7	10	1.00	2.33	2.50
Rodents.....	16	28	31	41	110	203	2.56	3.93	6.45
Carnivores.....	9	15	17	10	29	51	1.11	1.93	3.00
Insectivores...	3	5	6	3	12	20	1.00	2.40	3.33
Cheiroptera...	4	7	11	7	12	26	1.75	1.71	2.36
Totals.....	34	58	68	63	170	310	1.85	2.93	4.56

crease of genera, and the constantly increasing addition of species as the area is enlarged.

By comparing the upper zones of the San Jacintos with the San Jacintos as a whole, and the upper zones of the Sierras with the Sierras as a whole (see Table III), we find that increasing the life zones has in a lesser degree the same effect as increasing the geographic area regardless of zones; in other words, adding life zones tends to have the same effect on speciation as adding faunas and associations without life zones. The following table (derived from Table III) illustrates this:

Mammals	San Jac. (Upper Zones)	San Jac. (All Zones)	Sierras (Upper Zones)	Sierras (All Zones)
Genera.....	18	34	45	58
Species.....	20	63	100	170
Index of mod.....	1.11	1.85	2.22	2.93

Another rough test of the hypothesis was made in a comparison of the mammalian faunas of some of our

large continental islands and zoologic regions, the results being shown in Table IV. The data used in this table are

TABLE IV
SPECIATION OF MAMMALS IN VARIOUS CONTINENTAL ISLANDS AND ZOOLOGIC REGIONS

Data from Selater and Selater (1899)

Group	Africa (11,770,000 Sq. M.)		Australian Region (3,390,000 Sq. M.)		Australia (2,947,000 Sq. M.)		New Guinea (312,000 Sq. M.)		Madagascar (228,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Ungulates...	155	35							1	1
Rodents.....	196	41	69	8			18	5	13	7
Carnivores...	59	22							9	7
Insectivores..	73	8							20	9
Bats.....	101	19	83	26			39	16	21	12
Lemurs.....	8	3							36	11
Primates....	72	6								
Hyraces.....	14	1								
Elephants...	1	1								
Edentates...	6	2								
Marsupials...			144	36			36	14		
Monotremes.			5	3			3	2		
Totals.....	685	128	301	73	169	59	96	37	100	47
Index of mod- ification...	5.35		4.12		2.86		2.59		2.13	

by no means up to date, being taken from the summaries in Selater and Selater (1899), but the subsequent additions to the faunas of the places concerned, and the splitting up of genera and species, have probably been approximately proportionate in each of the five areas, and therefore the figures used are sufficiently accurate to be significant. Comparing Africa, the Australian region, Australia, New Guinea and Madagascar, which rank in size in the order given, we find that the indices of modification of their mammalian faunas are as follows: Africa 5.35, Australian region 4.12, Australia 2.86, New Guinea 2.59, and Madagascar 2.13. Certainly these figures are significant.

Comparing the mammalian faunas of the various islands of the Philippine Archipelago (Table V), we find that there is even here some corroboration of our law of

TABLE V

SPECIATION OF MAMMALS IN ISLANDS OF THE PHILIPPINE ARCHIPELAGO

Data from Hollister (1912)

Island	Sq. Miles	Sp.	Gen.	Index of Mod.
Luzon.....	40,969	72	40	1.80
Mindanao.....	36,292	61	32	1.90
Samar.....	5,031	16	13	1.23
Negros.....	4,881	14	13	1.07
Panay.....	4,611	10	8	1.25
Palawan.....	4,027	21	18	1.16
Mindoro.....	3,851	17	11	1.54
Leyte.....	2,722	9	8	1.12
Cebu.....	1,762	8	7	1.14
Bohol.....	1,441	3	3	1.00
Masbate.....	1,236	5	4	1.25

speciation. Considering the large element of chance in the animal population of a group of islands of such small size as those of the Philippines, where the various islets are at a varying distance from each other, and their faunas have originated from different sources, the relation between their size and the differentiation of their forms is remarkably regular. In Table V, where the main islands have been listed in order of size, with their numbers of genera and species of mammals, the deer have been excluded entirely, since their generic and specific differentiation is in too chaotic a state to be used. The most striking fact brought out by the table is the lead which the two large islands, Luzon and Mindanao, show, not only in total number of forms, but in index of modification as well. With the possible exception of Mindoro and Palawan, practically none of the smaller islands is supporting as large a variety of mammalian forms as could be expected of it, a fact which might be explained in a number of ways.

In all of the tabulations given, the marine mammals have been entirely excluded since the factors affecting their distribution and speciation are so different from those of terrestrial mammals. In the majority of cases marine mammalian families have a paucity both of genera and species, a circumstance brought about by a number of factors. Generally speaking, large, wide-ranging

forms, or forms which are poor in numbers of individuals, are poor in genera and species, possibly due to the comparative uniformity of their environment, which is usually coincident. Most marine mammals are of these kinds, and their paucity of types is emphasized by the comparative uniformity of their environment, even in the most widespread groups. From a distributional point of view, *i. e.*, taking into account life zones, faunas and associations, a cosmopolitan, oceanic, surface group of animals does not range through as great a variety of ecologic niches and environmental and climatic conditions as does a cosmopolitan terrestrial group.

In order to determine whether the principles of distribution and differentiation here set forth would apply to birds as well as to mammals, a number of series of comparisons was made as with mammals, and with exactly comparable results.

TABLE VI
SPECIATION OF BIRDS IN VARIOUS CALIFORNIA AREAS
Data from Grinnell (1913B), (1908), Willett (1912)

Group	San Bernardino Mts. (2,000 Sq. M.)		Southern California (30,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Passeres.....	62	82	79	114	87	197
Picariæ.....	16	20	19	23	20	38
Striges.....	3	3	7	7	8	15
Accipitres.....	5	5	10	14	12	17
Columbæ.....	1	1	2	2	3	3
Galli.....	1	1	3	3	6	11
Limicolæ.....	3	3	4	4	9	10
Grues.....	1	1	5	6	6	8
Waders.....	2	2	7	7	8	11
Anseres.....	2	2	5	5	11	11
Other water birds...	1	1	12	14	16	26
Total.....	97	121	153	199	186	347
Index of mod.....	1.25		1.30		1.87	

Table VI gives a comparison of genera and species of resident birds of (a) the San Bernardino Mountain region, (b) Southern California, and (c) California as a whole. Almost without exception, in each individual group of birds there is a reduction in the index of modi-

fication as the area is restricted from California to the Pacific Coast region of Southern California, and finally to the San Bernardino region. The totals reflect the trend in each group. While in the largest area the number of genera is considerably less than double what it is in the smallest, the number of species is more nearly tripled. The Southern California area is intermediate.

TABLE VII
SPECIATION OF RESIDENT BIRDS IN AUSTRALIA AND TASMANIA
Data from North (1901-1909)

Group	Australia (2,947,000 Sq. M.)			Tasmania (26,000 Sq. M.)		
	Sp.	Gen.	Fam.	Sp.	Gen.	Fam.
Passeres.....	304	119	26	53	42	15
Picariæ.....	29	18	6	7	7	3
Striges.....	9	2	2	1	1	1
Accipitres.....	27	17	2	11	9	2
Psittaci.....	57	14	3	11	9	3
Total.....	426	170	39	83	68	24
Index of generic mod.....	4.35			2.83		
Index of specific mod.....	2.30			1.22		

Table VII shows a comparison of the families, genera, and species of resident birds of Australia and Tasmania, from North (1901-1909). Here again, in addition to a very marked diminution of the total number of types in Tasmania as compared with Australia, each group shows a considerable decrease in the ratio of genera to families, namely, from 4.35 in Australia to 2.83 in Tasmania, and of species, to genera going from 2.30 in Australia to 1.22 in Tasmania.

Table VIII is a similar comparison of (*a*) the resident birds of Ireland, from Hartert (1912), (*b*) the resident birds of all the British Isles, from Hartert (1912), (*c*) all the species of the Palaearctic region, the great majority of which are resident in one part or another, from Dresser (1902), (*d*) all the species of Japan, many of which are not resident, from Ogawa (1908), and (*e*) all the species of Kamtschatka, where the majority are resident, from

TABLE VIII

SPECIATION OF BIRDS IN VARIOUS PALEARCTIC REGIONS

Data from Hartert (1912), Dresser (1902), Ogawa (1908) and Stejneger (1885)

Group	Ireland (32,583 Sq. M.)		British Isles (120,900 Sq. M.)		Palearctic Region (19,150,000 Sq. M.)		Japan (147,700 Sq. M.)		Kam- tschatka (105,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Passeres.....	57	35	85	42	610	116	180	64	55	38
Picariæ.....	4	4	7	7	81	21	34	16	8	5
Striges.....	2	2	5	4	34	11	14	8	4	3
Accipitres.....	7	4	12	7	66	21	23	14	15	7
Columbæ.....	4	2	4	2	29	6	12	6	0	0
Galli.....	4	4	8	7	76	19	11	5	5	3
Limicolæ.....	10	9	15	11	97	32	45	21	25	17
Grues.....	4	4	5	5	34	13	27	9	1	1
Waders.....	1	1	1	1	31	12	23	12	0	0
Anseres.....	8	8	16	12	64	24	39	21	28	20
Other water birds.....	23	14	30	15	129	35	83	28	32	18
Total.....	124	87	188	113	1,251	310	491	204	183	112
Index of mod.....	1.42		1.66		4.00		2.40		1.63	

Stejneger (1885). The increase in index of modification from Ireland to the British Isles, and then to the entire Palearctic region, is almost exactly what should be expected. The greater number of both genera and species in Japan as compared with Kamtschatka reflects the greater variety of ecologic niches in a warm country as compared with a cold one of comparable size. A comparison of the *resident* species of Japan with the resident species of the British Isles would be of very great interest, but such a list of Japanese birds is not available. The very striking similarity between the speciation of birds in Kamtschatka, and that in the British Isles, both in number of genera and of species, is very remarkable. The interesting manner in which the balance of nature is preserved is shown by the large representation of raptorial birds to parallel the abundance of shore birds and Anseres.

That reptiles and amphibians are influenced in their speciation by their distribution is indicated by Table IX, which shows a comparison of the genera and species of amphibians, lizards, and snakes, in three of the geographic areas defined by Cope (1898).

TABLE IX

SPECIATION OF AMPHIBIA AND REPTILIA IN NORTH AMERICAN AREAS

Data from Cope (1889), (1898)

Group	Lower California District (12,000 Sq. M.)			Western Sub-region (500,000 Sq. M.)			Medicolumbian Region (4,500,000 Sq. M.)		
	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.
Amphibia.....	4	3	1.25	23	10	2.30	130	28	4.64
Lacertilia.....	17	13	1.30	28	13	2.15	143	31	4.61
Ophidia.....	16	12	1.33	20	9	2.22	191	45	4.24

The "Lower California district" consists of only the tip of Lower California; the "Western subregion" embraces the Pacific slope of North America from Northern Mexico, east of the Sierras, to Oregon, where it crosses the Sierras to the Rocky Mountains, including northern Idaho, eastern Montana, and most of British Columbia. The "Medicolumbian region" includes northern and central Mexico, and most of the United States and Canada north to a line drawn diagonally from New England to Alaska, interdigitating on its border with the "Holarctic region."

The almost exactly parallel increase in the indices of modification in the three groups of cold-blooded vertebrates considered, as the area is extended, is quite remarkable. All three groups average from 1.25 to 1.33 species per genus in the smallest area, from 2.15 to 2.30 in the intermediate area, and from 4.24 to 4.64 in the largest area.

As suggested by Professor Kofoed, a factor influencing speciation in such diverse vertebrates as mammals, birds, reptiles, and amphibians, should be very widely applicable to speciation in the entire animal kingdom.

A series of statistics relating to various orders of insects and other invertebrates has been compiled to ascertain whether in these groups as well as in vertebrates, the number of species increases out of proportion to the genera, as the size of the area, in a distributional sense, is enlarged.

TABLE X
SPECIATION OF ELATERIDÆ IN VARIOUS AREAS OF UNEQUAL SIZE
Data from Schwarz (1906)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
Africa.....	11,770,000	574	55	10.43
Madagascar.....	228,000	245	36	6.80
India.....	1,760,000	438	53	8.26
Borneo.....	296,700	150	40	3.75
Sumatra.....	184,000	177	41	4.31
Java.....	50,000	125	35	3.37
Ceylon.....	25,333	96	28	3.42
Australia.....	2,947,000	386	42	9.19
New Guinea.....	312,000	61	20	3.05
New Zealand.....	104,750	137	24	5.70
Tasmania.....	26,000	13	7	1.86

Table X was compiled to show the number of genera and species of beetles of the family Elateridæ in various continents and islands, the regions chosen for comparison being well defined areas of unequal size.

A careful inspection of this table shows that with only two exceptions the indices of modification are directly proportional to the size of the areas. Borneo and New Guinea, however, not only show a smaller index of modification than should be expected of them, but are poor in total number of types. Nevertheless, when we reflect that these two islands are not nearly so thoroughly known to science as are the other areas considered in the table, no great significance can be attached to their seeming paucity of known types.

Table XI shows the number of genera and species of Limnophilidæ, a family of Trichoptera, in eastern North America (east of the Rockies) as compared with North America as a whole. It will be noticed that while in the

TABLE XI
SPECIATION OF LIMNOPHILIDÆ (TRICHOPTERA) IN NORTH AMERICA
Data from Ulmer (1907)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
North America.....	8,000,000	98	27	3.63
Eastern North America....	5,000,000	45	20	2.25

larger area the number of species is more than double what it is in the smaller area, the increase in genera is only about one third, increasing the index of modification from 2.25 to 3.63.

Table XII shows practically the same thing in the case of the hawk moths of the family Sphingidæ.

TABLE XII

SPECIATION OF SPHINGIDÆ IN AMERICAN AND AFRICAN AREAS

Data from de Rothschild and Jordan (1907)

Area	Sq. Miles	Sp.	Gen.	Index of Mod.
West Indies.....	76,000	61	20	3.05
Mexico and Central America.....	975,200	122	34	3.58
South America.....	7,000,000	197	35	5.62
Mex., Cent. Am., and S. Am.....	7,975,200	237	40	5.92
Mex., Cent. Am., S. Am., and W. I....	8,051,200	262	41	6.39
Bourbon.....	965	7	5	1.40
Madagascar.....	228,000	39	20	1.95
Africa.....	11,772,000	166	48	3.45
Africa and Mad.....	12,000,000	195	53	3.67
Africa, Mad., and Bourbon.....	12,000,965	197	53	3.71

In this case two series of tabulations were made, one showing the number of genera and species in various Neotropical areas, and combinations of these areas, the other showing a similar tabulation for various Ethiopian areas, with similar combinations. It will be observed that the speciation in the West Indies is very large for the size of the area involved, but when we consider the abundant opportunity that has been given for isolation to operate, this is not surprising. The index of modification is quite low. Mexico and Central America have a larger speciation, compared with South America, than would normally be expected, the reason being that Central America is the American center of distribution. The index of modification, however, reflects the smaller size of the area, being considerably lower than that for South America. The increase in index of modification from 5.62 to 6.39, as areas are successively added to South America, is significant. Looking now at the Ethiopian regions, we find that there is the same disproportionate increase of species over

genera in successively larger areas, the index of modification increasing from 1.40 in the small island of Bourbon to 1.95 in Madagascar, and 3.45 in Africa. Combining Africa and Madagascar, this is increased to 3.67, and with the island of Bourbon, to 3.71.

Table XIII is one of especial interest, since it deals

TABLE XIII
SPECIATION OF MARINE GAMMARIDEA (AMPHIPODA) IN VARIOUS SEAS
Data from Stebbing (1906)

Area	Sp.	Gen.	Index of Mod.
Mediterranean Sea.....	147	67	2.19
Arctic Ocean.....	311	140	2.22
N. Atlantic Ocean.....	475	176	2.70
S. Atlantic Ocean.....	65	44	1.47
Arctic and N. Atlantic.....	588	191	3.07
Arctic, N. Atlantic, and S. Atlantic.....	645	207	3.11
Arctic, N. Atlantic, S. Atlantic and Med. Sea.....	735	214	3.43
Whole family.....	1,333	313	4.22

with a marine instead of a terrestrial group. It embodies the results of a compilation of the marine genera and species of Amphipoda of the suborder Gammaridea in a number of the oceans and seas of the world. Since it is primarily a cold-loving group, the largest numbers are found in the cold seas, the Arctic and North Atlantic being the home of considerably over half of the known marine species. It is very likely that when the Antarctic regions have been studied as thoroughly as the northern regions, the number of species from that part of the world will be very considerably increased. At the time of Stebbing's work on Amphipoda, our knowledge of Antarctic and contiguous areas was very meager.

The steady increase of the index of modification from the smaller to the larger seas is striking. The Mediterranean Sea, although it is the most thoroughly known of all, has the lowest index of modification, namely 2.19, the Arctic Ocean comes next with 2.22, and then the North Atlantic with 2.70. The small number of species from the South Atlantic and Antarctic regions has already been

mentioned, and its low index of modification may be attributed to the same sort of imperfect knowledge as in the case of Borneo and New Guinea in Table X. The constant growth of the number of species per genus from 2.22 to 3.43 as the various seas and oceans are added together, exactly parallels the results obtained in a similar way for a terrestrial group in Table XII. The comparison of the speciation of the largest area for which it was worked out, with the speciation of the entire group, many species and genera of which inhabit fresh water, is interesting, jumping as it does from 3.43 to 4.22. From the facts brought to light by this table it can hardly be doubted that practically the same influence is brought to bear on the speciation of marine as on terrestrial organisms by the extent of their distribution.

The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, effect of time, causes of specific and generic modification, etc., each of which will be dealt with in the following pages as they seem to influence the law here proposed.

Let us first consider the factor of isolation in relation to the production of new forms. As excellently stated by Cook (1909), isolation can not be considered as a cause or factor in evolution, since changes in the characters of species are not dependent upon the subdivision of species to form additional species. To quote from him:

The separation of species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes of the same kind would take place if the species were not divided. That the isolated groups become different, does not indicate that isolation assists in the process of change. It gives the contrary indication that changes are restricted by isolation. If isolation did not confine the new characters to the group in which they arise, the groups would remain alike, instead of becoming different. . . . Isolation is the shears that splits the species, not the loom that weaves it.

Therefore, while isolation can not be considered a factor in evolution, it is an important factor in speciation. Species vary in many directions or orthogenetically pro-

gress in a definite direction, but the trend of variation or progression may be different in one locality, and tend towards a different result, from that of another locality. Whether the evolution, usually in more or less divergent directions, of segregated groups of individuals be looked upon (1) as the accumulation of numerous slight variations which have a different average character in any two portions of a species, as originally explained by Darwin (1859, Chap. 4) or (2) purely as the result of natural selection, as argued by Wallace (1858), or (3) as the result of a change in the average character of two portions due to the uneven occurrence of mutations in the two portions, a conclusion reached by Dewar and Finn (1909, p. 380), or (4) as the result of orthogenetic evolutionary tendencies inherent in the species and influenced by the environment, as Eimer suggested (1897, Chap. 1), does not concern us here,—the general tendency appears to be that two isolated portions of a species as a general rule trend in different directions, and diverge farther and farther as long as they are isolated.

It is assumed that the greater the length of time given for the influence of isolation to be felt, the farther apart are the two originally identical divisions likely to trend, however the dissimilar evolution be interpreted. As stated by Tower (1906), in speaking of the method of evolution of the Chrysomelid genus *Leptinotarsa*,

We can interpret the conditions found by any of the current hypotheses; but explaining a condition by an hypothesis is not the same as that the conditions found are evidence in support of an hypothesis, although it is often so used.

The existence of distinct variations, subspecies, and ultimately species and genera, in isolated areas is a too frequently observed phenomenon to be looked upon as anything else than a self-evident truth, but that this should necessarily be considered as supporting any particular theory of evolution can not be argued.

The profound results of prolonged isolation may be observed in the fauna of some of our long-separated con-

tinental islands, such as Madagascar, Australia and New Zealand. Decreasing degrees of isolation may be observed in our West Indian islands, where some generic differentiation has occurred; in the Santa Barbara islands, where there has been a differentiation of species; and the detached mountain ranges of Southern California, where the upper life zones are at present in an isolated condition, but have been so only long enough to develop a few new subspecies, and to lose many of the types of the mother range, in accordance with the law proposed by Grinnell and Swarth (1913) that "the smaller the disconnected area of a given zone, or distributional area of any other rank, the fewer the types which are persistent therein."

From this it is apparent that the time element, in conjunction with isolation, may have a very decided effect on the number of genera and species in a family, but since, from a geologic point of view, animals appear to have reached a new equilibrium very quickly after a geographic change, the time element may have little effect on the numbers of genera and species relative to each other in any given area. In other words, as fast as new genera are produced in a given area, the species within the genera will tend to be produced in the same ratio, thus leaving the index of modification unaffected.

As an example of the effect of time and isolation let us take a hypothetical case. Let us assume that a certain island became divided into two islands of unequal size, and that after a short period of segregation, just long enough for the fauna to readjust itself to the smaller areas and reach a new equilibrium, we had say six species in three genera on the larger island, and three of the same species in two of the genera on the smaller one. After a long period of isolation we should have approximately the same number of genera and species on the two islands, but they would have diverged to generic differentiation. In other words, the effect of time in conjunction with isolation is to increase the number of genera and species in the family, while the index of modification undergoes little change.

This leads us to a consideration of the factors involved in the differentiation of genera as contrasted with the differentiation of species. In general it may be said that extrinsic modifications, *i. e.*, those which are in some way connected with changes in temperature, humidity, character of flora, food, and other environmental conditions, and which usually affect such characters as color, size, length of hair, etc., lead to differentiation of species and subspecies primarily. On the other hand, intrinsic modifications, *i. e.*, those which are related directly or indirectly to a change in the habits or mode of life of the animal or the occupation of a new niche in nature, usually, if not always, lead to generic or family differentiation, since it is evident that changes fitting an animal to live arboreally instead of terrestrially, for instance, are of such a nature, that if they are perpetuated and carried to perfection, will not stop at specific difference but will become of generic importance.

It might be argued that there are no modifications which might not, if carried far enough, ultimately lead to generic differentiation. This is possible, but very improbable, because the modifications here alluded to as "extrinsic" are of such a nature that in the varying climatic conditions there are likely to be intermediate forms which make the division of the more widely separated ones into genera impracticable. In the case of our "intrinsic" modifications, intermediate forms are not so likely to exist when once the incipient changes leading to an altered mode of life have reached a fair degree of perfection.

As a concrete example of what is meant by extrinsic and intrinsic modifications, let us take the squirrels of a given region, say eastern North America. There are four genera to be distinguished,—*Sciurius*, *Tamias*, *Sciuropterus* and *Arctomys*. The genus *Sciurus* contains strictly arboreal, mostly nut-eating, omnivorous forms. *Tamias* includes forms which are terrestrial, diurnal, dwelling in natural or artificial holes and crevices, and with a device for carrying food in their cheeks. *Sciuro-*

pterus is an arboreal type which is nocturnal, and has developed characters which enable it more easily to travel from tree to tree. *Arctomys* is the most highly modified form, and has departed most widely in its habits; it is entirely terrestrial, seeks shelter in artificial burrows, eats grass, and hibernates.

Were we to study the characters separating these genera, we should find that they are all characters which enable the animal best to occupy the ecologic niche it fills. If now we select any one of these genera and examine its species, we perceive that the differences we find are not such as could clearly be related to differences in mode of life or habits, but rather such differences as are induced by the circumstances mentioned above, such differences being size, color, length of feet and tail, texture of fur, etc.—i. e., extrinsic variations.

An interesting example of both extrinsic and intrinsic modifications in an incipient stage may be found in the song-sparrows of western United States. Let us compare the form of the humid northwest coast belt, *Melospiza melodia morphna*, with the form of the arid Arizona deserts, *M. m. fallax*. The differences to be observed in color and size are very noticeable, and would undoubtedly lead to their separation into two distinct species were it not for the complete chain of intermediate forms. But even if the chain of intermediate forms were not complete, and after a period of segregation the numerous intergrading subspecies became broken up into a few well-marked species, nevertheless, unless a change in mode of life of the bird were involved, however far the extremes of color and size might tend, they could not be given generic distinction because of the intermediate forms, inhabiting semi-arid or semi-humid regions, which would be almost certain to exist. It happens, however, that *Melospiza melodia morphna*, and *M. m. fallax*, do differ considerably in mode of life, the former being a beach comber, the latter a nomad of the desert. It would be expected, therefore, that if these two subspecies were isolated, the modifications re-

lated to their difference in mode of life, already shown in an incipient manner, would soon lead to their generic differentiation.

It is not argued that under a given set of ecologic conditions, only one type could be produced, nor that according to the idea of some zoologists, as set forth and refuted by Grinnell and Swarth (1913), should individuals of one geographic race be transplanted into the region of a different geographic race, the first race would assume within a few generations all the characters of the second race. Whether the changes due to the influence of the environment be looked upon as the results of natural selection and adaptation, or merely as the results of a stimulus to the germ plasm, the new type would not necessarily be always the same, this, however, depending upon the number of potential responses in the type, and, as excellently shown by Ruthven (1909) in his study of evolution in the genus *Thamnophis*, upon the modifications previously undergone by the type we are dealing with.

It is very evident that there are many variations in animals which seem to fall into neither the extrinsic nor intrinsic category, but which are neutral and vary independently of climate or habits, and may be inherited phylogenetic tendencies. It is very largely due to these neutral variations, frequently to be ascribed to orthogenetic evolution, tending in different directions in different places, and given an opportunity to diverge by isolation, that different species may be produced to occupy regions of similar climatic and environmental conditions, and different genera may be found occupying the same ecologic niches.

To choose an example in the same family quoted before, we may cite the case of *Tamias* in eastern North America, and *Eutamias* in western North America. In this case the characters separating the genera are not clearly related to their mode of life, the chief difference being the loss of one small premolar in *Tamias*, and its retention in *Eutamias*. The extent of divergence of these neutral varia-

tions depends on the duration of *geographic* segregation, and may therefore be of specific, generic, family, or ordinal rank.

To sum up, specific modifications may be of three kinds: (1) extrinsic modifications, induced by changes of climate and environmental conditions; (2) neutral modifications, due to a different trend of evolution in segregated regions; (3) incipient generic modifications. On the other hand, generic modification may be either intrinsic modifications, concomitant with changes in mode of life or habits of the animal, or neutral modifications as above, given generic value by a longer period of segregation.

Having dwelt for some length on these preliminary considerations, let us now apply them to the case in hand and see how they affect differentiation into species and genera through extension of range.

It is a well-known biological fact that different types of a group of animals, at least of higher animals, are found associated with different environments; nearly related species do not, as a rule, live comfortably together in the same environment, and nearly related genera do not occupy the same ecologic niche in a given zoogeographical area. This does not seem to hold true for animals of lower organization, as conclusively shown by Kofoed (1907). It is common for a group of animals, unless hindered by an impassable barrier or unfavorable environmental conditions, not only to continually extend its range into new territory, but also to attempt to live in as many different niches in nature as possible within a given area. Such attempts to invade new ecologic niches are frequently concomitant with heritable modifications better fitting them to occupy their new situation, though it is difficult to say whether these modifications are causes or results of the change in mode of life. However this may be looked upon, the tendency to occupy new niches in nature is frequently accompanied by intrinsic modifications, and therefore by generic differentiation.

From this we may safely assume that in a given area

a family of animals, by adaptive evolution, will approach a maximum of generic differentiation which can be supported in that area. In other words, every suitable ecologic niche which is represented in the region considered will be invaded by the family, and even in a small area there is likely to be a considerable generic differentiation, especially if isolation has had any opportunity to operate within the area, in breaking up the genera and species.

Let us assume that in one unit of area a certain family, Sciuridae for example, was represented by three genera, each with three species. Second, let us assume that this family kept spreading into additional units of area. With each new unit, the chance of new suitable ecologic niches being represented would decrease, and therefore the chance of new genera being represented would decrease, since if a genus were fitted for its niche in nature under certain conditions of climate and environment, it would in the majority of cases not be likely to undergo any radical changes in the occupation of the same niche under somewhat altered conditions of climate and environment; *i. e.*, the stimulus for intrinsic modification would be lacking.

On the other hand, with each additional unit of area, the chances of the combined conditions of temperature, humidity, and environment being different, would remain the same. In other words, the chances of the three dimensions influencing the life of a region, *i. e.*, "life zone" (controlled by temperature), "fauna" (controlled by humidity), and "association" (controlled by the effect of the other two plus a number of other environmental conditions), intersecting at the same point would be almost equally improbable with each succeeding unit of area. Since it is changes in "life zone," "fauna," or "association" which produce extrinsic changes, and therefore lead to differentiation of species and subspecies primarily, the increment of species would average nearly the same for each succeeding unit of area, other factors remaining equal. It should also be taken into consideration that

with the invasion of new zoogeographic areas, contact with allied forms is frequently experienced, and opportunity is thus afforded for cross breeding and hybridization, the result of which upon the germ plasm appears to be as influential in the production of new forms as is the shock of new environmental conditions. The constant increase in species and subspecies accompanying invasion of new territory, going hand in hand with a diminishing increase in genera, results in the constantly larger index of modification as the area inhabited by a group is extended.

SUMMARY

1. Extent of distribution has a direct influence on the speciation of the group concerned in this way, that as the range of a group of animals is extended, the species increase out of proportion to the genera, the genera out of proportion to the families, and the families out of proportion to the orders.

2. Comparison of different families having unequal geographic ranges is usually inaccurate due to the great differences in the other factors controlling their speciation. Those families which do lend themselves to such a comparison show decidedly the effect of extent of distribution, *e. g.*, the bats and some of the insectivores, the families of widest distribution having the largest indices of modification. A number of exceptions exist in the form of certain wide ranging genera which have a paucity of species. We have no adequate explanation for this phenomenon.

3. Comparison of the faunas of areas of different size gives very accurate results. A number of tabulations show as a whole an invariable increase in the index of modification as the distributional area is extended by the addition of either life zones, faunas, or associations. Such tabular comparisons were made for all the classes of terrestrial vertebrates, for several families of insects, and for the marine Amphipoda of the suborder Gammaridea. Allowing for explicable exceptions, the increase in number

of lower systematic groups out of proportion to the increase of higher systematic groups as the area considered is enlarged is a remarkably constant and wide-spread phenomenon.

4. The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, the time element, and causes of specific and generic modification.

5. Isolation is an important factor in speciation, since the separation of species into two or more parts allows the parts to become different. The degree of divergence of the segregated parts is largely dependent upon the duration of segregation.

6. Time, in conjunction with isolation and evolution, tends to increase the number of genera and species in a family, but the index of modification, *i. e.*, the average number of species per genus, remains approximately the same in a given area.

7. Three types of modifications in animals may be named:—first, “extrinsic” modifications, which are induced by climate and other environmental conditions, and which lead to differentiation of species and subspecies primarily; second, “intrinsic” modifications, which are concomitant with a change in habits or mode of life of the animal, due to the occupation of a new ecologic niche, and which usually lead to generic or family differentiation; and third, neutral modifications, which are merely the result of the natural tendency of all animals to vary and to be subject to more or less orthogenetic evolution,—modifications which can not be correlated with environmental conditions, nor with a change in mode of life of the animal, but which may be influenced largely by inherited tendencies. Such modifications are responsible for the production, through isolation, of different species to live under the same climatic and environmental conditions, and of different genera to occupy the same ecologic niche.

8. Specific modifications may be of three kinds: (1) ex-

trinsic modifications, (2) neutral variations in segregated regions, (3) incipient generic modifications. Generic modifications may be (1) intrinsic modifications, or (2) neutral variations, given generic value by a longer period of segregation.

9. Since different types of a group of animals are usually found associated with different environmental conditions or different ecologic niches, and since it is common for animals, if unhindered, not only to extend their range continually into new territory, but also to occupy new ecologic niches, and since these tendencies lead to specific and generic differentiations, respectively, any given area will have a differentiation of species proportionate to its variety of environmental conditions, and of genera proportionate to its variety of suitable ecologic niches.

10. Since, as the area of distribution is extended, the chance of new conditions of climate and environment being represented remains approximately the same, the increase in number of species is nearly proportional to the increase in the area of distribution, but since the chance of new ecologic niches being represented in most cases constantly decreases, the increase in genera proceeds at an ever-diminishing rate. This, going hand in hand with the nearly constant increase in species or subspecies, results in a constantly increasing index of modification.

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